

On *Leptophoca* and *Prophoca* (Pinnipedia, Phocidae) from the Miocene of the North Atlantic realm: redescription, phylogenetic affinities and paleobiogeographic implications.

Leonard Dewaele^{1,2,*}, Olivier Lambert¹, Stephen Louwye²

¹O.D. 'Earth and History of Life', Royal Belgian Institute of Natural Sciences. 29 Rue Vautier, Brussels 1000, Belgium.

²Research Unit Palaeontology, Department Geology. 281 Krijgslaan – S8, Ghent 9000, Belgium.

* leonard.dewaele@ugent.be

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Prophoca and *Leptophoca* represent the oldest known genera of phocine seals, dated from the latest early to middle Miocene. Originally, *Prophoca rousseaui* and *Prophoca proxima* were described based on fragmentary postcranial remains from the Miocene of Belgium, whereas *Leptophoca lenis* and *L. amphiatlantica* were later named based on specimens from the east coast of North America and from both the Netherlands and the east coast of North America, respectively. However, multiple researchers contested the union of *P. rousseaui* and *P. proxima* into the same genus, without stating much evidence. Furthermore, the stratigraphic context of the genus *Prophoca* remained poorly constrained due to the lack of precise data associated to the specimens collected in the area of Antwerp during the second part of the nineteenth century.

Prophoca rousseaui specimens from Belgium are redescribed and *Prophoca proxima* is considered synonymous to *Leptophoca lenis*, with the proposal of a new combination *Leptophoca proxima* (Van Beneden, 1876). In previously published comparisons between *P. proxima* and *L. lenis*, differences including overall size, the shape of the posterior part of the diaphysis and the lesser tubercle were mentioned. However, a detailed comparison with extant seals indicates that these size and shape differences can be explained by intraspecific variation. Furthermore, newly illustrated and measured specimens of *L. lenis* show sizes and shapes intermediate between or overlapping with

the original *L. lenis* and *P. proxima* material. Following a re-investigation of *Leptophoca amphiatlantica*, some characters from the original diagnosis appear to fall within the range of natural variation of *L. proxima*. Other differences between both species remain, but their validity to separate *L. amphiatlantica* from *L. proxima* is questioned. Hence, the specimens of *L. amphiatlantica* are considered *Leptophoca* cf. *L. proxima*.

In a phylogenetic analysis including 95 characters and 21 taxa, *Prophoca rousseaui* and *Leptophoca proxima* constitute the earliest diverging clade of stem-phocines, a result that is relatively well supported.

Three dinoflagellate cyst biostratigraphic analyses of sediment samples associated with *P. rousseaui* and *L. proxima* from Belgium give age ranges of 14.2-13.2 Ma and 14.2-7.2 Ma for *P. rousseaui* and of 14.8-13.2 Ma for *L. proxima*. The latter slightly postdates the oldest known find of *L. proxima* from North America, allowing to propose that Phocinae originated along the east coast of North America during the late early Miocene and spread to Europe shortly after.

Morphological features of the appendicular skeleton, for example the relatively smoothly-shaped deltopectoral crest and the relatively straight diaphysis of the humerus, indicate that *Prophoca rousseaui* and *Leptophoca proxima* are functionally primitive seals, retaining a more prominent use of the fore flipper for aquatic propulsion than extant Phocidae.